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INTRODUCTION

In contrast to plants and animals, studying spatial patterns is recent for microorganisms and most studies in terrestrial ecosystems have been conducted at the field scale. However, the spatial scale at which patterns are investigated is of fundamental importance since it is well known that patterns can change with the scale of description. A landscape perspective is needed to understand the impact of human activities on natural habitats and ecosystems which implies investigating spatial patterns over broad spatial scales. How microorganisms are spatially distributed at the landscape scale and which factors, among land management, soil physico-chemical properties and local climate govern their distribution are therefore central, yet unanswered, questions despite the fact that microbial communities are essential for biogeochemical cycling and ecosystem functioning.

Here, we characterized and explained the spatial variability in the distribution of microbial communities involved in nitrogen cycling at the landscape-scale using canonical variation partitioning and geostatistical modeling.

CONCLUSIONS

The largest variations in gene copy numbers across the 31 500 km2 of the Burgundy region were observed for the ammonia-oxidizing crenarchaeota (*AOA*) and total crenarchaeota (Fig. 1). In accordance with the study of Leininger et al. (2006), we found that the abundance of the *AOA* and the total crenarchaeota were highly correlated (R^2=0.72, P<0.001).

Using a dataset describing 49 different soil and environmental variables at each sampling site (Table 3), we found that ***between 55% and 85 %*** of the spatial variance in the distribution of the studied communities could be explained (Table 1).

When grouping the variables into 5 categories (spatial effects, land use, climate, soil physics and soil chemistry), and calculating the partial redundancy analysis models for each dataset, soil chemistry was the strongest predictor and explained between 17% and 59% of the total variance (Table 1).

When separating the effect of each variable, pH emerged as either an important or the strongest single soil chemistry predictor for most communities (Table 2).

Three dominant types of ecosystems were distinguished across the 107 Burgundy sites with forests, grasslands and agricultural soils dominating. but changes in land use did not strongly influence the abundance of any of the studied communities other than the *AOB*,

Investigating the spatial correlation of microbial abundance using a geostatistical approach revealed strong spatial patterns in the distribution of some communities with autocorrelation ranging between 3 and 140 kilometers (Fig. 2).

This study highlights the potential of a spatially explicit approach to identify the overarching factors driving the spatial heterogeneity of microbial communities even at the landscape scale.

Table 1. Partitioning of the biological variation of different microbial communities as a function of contextual parameters

	Overall model[a]			Respective contribution of contextual variables (% explained variance)[b]					
	N	F-ratio	Total explained variance (%)	Space	Land use	Climate	Time	Soil physics	Soil chemistry
Total Bacteria	16	14.81***	73.1	7.70***		19.7***		6.5***	20.8***
Total Crenarchaea	16	27.01***	85.1	1.3**	1.6*	0.3^{ns}		1.4*	25.2***
Nitrate reducers									
narG	25	17.33***	55.0	14.6***		1.4*	0.6^{ns}	2.3**	39.1***
napA	16	10.89***	66.7	6.0**			6.6**	3.9**	49.5***
Denitrifiers									
nirK	12	18.64***	71.1					2.8**	59.3***
nirS	21	16.99***	83.0	2.2**	0.5^{ns}	1.6**	2.1**	1.2*	35.5***
nosZ	10	17.08***	64.7	3.8**		5.2**		2.3*	41.3***
Nitrifiers									
AOB	8	22.59***	70.8		18.6***			1.3*	16.9***
AOA	15	25.65***	83.5		1.1^{ns}			0.9*	26.9***

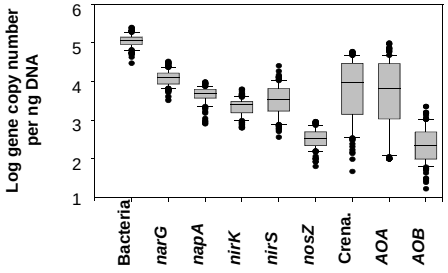

Fig.1. Variation in the abundance of different microbial communities across the Burgundy region.

Table 2. Contribution of the first five most important explanatory variables to the spatial variation

	% variance explained by:				
Total Bacteria	pH (17.8)	Tp_{tot} (13.1)	Sp. $Dist._y$ (7.1)	Rain (6.0)	Cr_{ext} (6.0)
Total Crenarchaea	pH (9.6)	K_{tot} (5.6)	Mg_{tot} (4.5)	Res.water (3.8)	Cd_{ext} (3.3)
Nitrate reducers					
narG	Carbon (7.6)	pH (7.1)	Sp.$Dist_{Y11}$ (5.6)	Sp.$Dist_{Y7}$ (4.5)	Mn_{exch} (4.2)
napA	Mn_{exch} (7.4)	Time (6.6)	Pb (6.2)	Sp. $Dist._x$ (6.0)	Cu_{ext} (5.2)
Denitrifiers					
nirK	pH (21.4)	Cu_{tot} (7.3)	Cr (6.0)	Fe_{tot} (5.4)	B (5.1)
nirS	pH (15.6)	Mn_{exch} (6.4)	Mn_{tot} (4.8)	Ca_{tot} (4.5)	Na_{tot} (2.8)
nosZ	pH (15.9)	Mn_{exch} (8.5)	Na_{exch} (5.7)	K_{tot} (5.5)	Tp_M (5.2)
Nitrifiers					
AOB	Land use (18.6)	Carbon (8.4)	Ni (6.6)	Na_{exch} (5.3)	K_{exch} (3.3)
AOA	pH (8.5)	K_{tot} (5.5)	Mg_{tot} (3.6)	Pb_{tot} (3.2)	P_{ass} (2.7)

Table 3 : Climate and soil properties across sites

data	*mini*	*max*	*mean±SD*	data	*mini*	*max*	*mean±SD*
Temp. month (°C)	2.5	20	9.6±4.8	**Mn exch**	-0.005	0.5	0.07±0.08
Rain month (mm)	41	109	72±17	**Al tot** (g^{-1} Kg)	0.26	0.9	0.53±0.17
PET month	14	149	58±33	**Ca tot** (g^{-1} Kg)	0.008	1.9	0.18±0.34
Temp. year (°C)	10.1	12.4	11.8±0.46	**Fe tot** (g^{-1} Kg)	0.079	0.65	0.28±0.13
Rain year (mm)	736	1361	914±120	**K tot** (g^{-1} Kg)	0.036	0.42	0.18±0.09
PET year	678	896	776±38	**Mg tot** (g^{-1} Kg)	0.007	0.12	0.04±0.02
Residual Water	6	88	27.3±16.1	**Na tot** (g^{-1} Kg)	0.005	0.19	0.04±0.04
Clay (g^{-1} Kg)	73	733	310±154	**Cd tot** (mg^{-1} Kg)	0.03	5.5	0.5±0.7
Fine Loam (g^{-1} Kg)	73	445	261±84	**Co tot** (mg^{-1} Kg)	1.5	37.3	12.5±6.5
Coarse Loam (g^{-1} Kg)	31	360	155±76.5	**Cr tot** (mg^{-1} Kg)	9.3	156	59.5±28.8
Fine Sand (g^{-1} Kg)	7	348	91±67.9	**Cu tot** (mg^{-1} Kg)	2.2	144	15.3±16.9
Coarse Sand (g^{-1} Kg)	2	772	183±172	**Mn tot** (mg^{-1} Kg)	170	4930	883±660
Carbon tot (g^{-1} Kg)	7	104	28.5±20.3	**Mo tot** (mg^{-1} Kg)	0.2	6.2	0.9±0.8
Nitrogen tot (g^{-1} Kg)	0.7	6	2.3±1.3	**Ni tot** (mg^{-1} Kg)	3.2	79	27±15.9
C/N	10	16	11.5±1.4	**Pb tot** (mg^{-1} Kg)	16	197	41.2±24
Calc tot	0.5	460	34.7±81.8	**Tl tot** (mg^{-1} Kg)	0.24	17	1.4±1.8
pH	4.2	8	6.4±1.2	**Zn_tot** (mg^{-1} Kg)	24	1231	99.3±122.5
P ass (g^{-1} Kg)	-0.01	0.2	0.041±0.035	**B ext** (mg^{-1} Kg)	0.1	0.7	0.2±0.1
CEC	3.0	56	17.6±13.7	**Cd ext** (mg^{-1} Kg)	0.02	2.4	0.24±0.3
Ca exch	0.2	56	16.5±14.6	**Cr ext** (mg^{-1} Kg)	-0.05	0.7	0.14±0.12
Mg exch	0.08	3	0.8±0.4	**Cu ext** (mg^{-1} Kg)	0.25	68	3.4±7.6
K exch	0.08	1.1	0.4±0.2	**Ni ext** (mg^{-1} Kg)	0.1	6.2	1.3±1.1
Na exch	0.014	0.2	0.05±0.03	**Pb ext** (mg^{-1} Kg)	2	55	7.8±6.6
Al exch	0.001	6.8	0.55±1.3	**Zn ext** (mg^{-1} Kg)	0.6	108	4.3±11.9

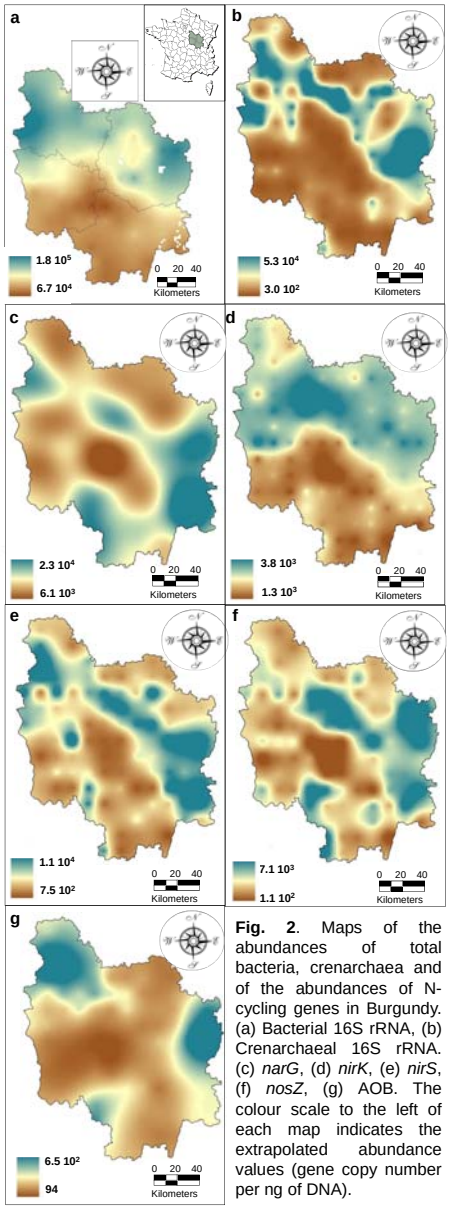

Fig. 2. Maps of the abundances of total bacteria, crenarchaea and of the abundances of N-cycling genes in Burgundy. (a) Bacterial 16S rRNA, (b) Crenarchaeal 16S rRNA. (c) *narG*, (d) *nirK*, (e) *nirS*, (f) *nosZ*, (g) AOB. The colour scale to the left of each map indicates the extrapolated abundance values (gene copy number per ng of DNA).

MATERIAL AND METHODS

The 107 sampling site locations were based on a 16×16 km systematic grid covering the Burgundy region. At the center of each 16×16 km cell, 25 individual core samples were taken of the topsoil (0–30 cm), using a random sampling design within a 20×20 m area and pooled. At each site, 42 soil physico-chemical properties were measured (Table 3).

The total bacterial and crenarcheal communities were quantified using 16S rRNA primer-based qPCR assays described previously (Ochsenreiter et al., 2003). Quantification of the bacterial and crenarcheal ammonia-oxidizers was performed according to Leininger et al. (2006) and Tourna et al. (Tourna et al., 2008) while quantification of nitrate reducers and denitrifiers was performed according to Bru et al. (2007) and Henry et al. (2006).

Data were anaylysed by Principal Coordinate of a Neighbor Matrix (PCNM) approach (Borcard et al., 2002) and the respective effects of each explanatory variable, or combinations thereof, were determined by canonical variation partitioning (Ramette et al., 2007). Spatial analyses were performed using the spatial analysis GeoR package (Ribiero et al., 2001)